



NOTES ON A PARTIAL SKELETON OF *MOURASUCHUS* (CROCODYLIA, NETTOSUCHIDAE) FROM THE UPPER MIOCENE OF VENEZUELA ¹

(With 9 figures)

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ABSTRACT: The specimen MCC 110-72V housed in the Museo de Ciencias Naturales de Caracas, Venezuela, is here described. This material, probably a specimen of *Mourasuchus arendsi*, is an associated but incomplete skeleton from the Urumaco Formation collected in 1972 by a joint field party with Venezuelan and North-american institutions. Bones are poorly preserved, all elements having suffered from chemical weathering during diagenesis and surface exposure. The lithology at the site is described as a gray, highly gypsiferous shale. The specimen consists of the skull and lower jaw, a substantial part of the vertebral column, fragments of ribs, parts of the pectoral and pelvic girdles, and some osteoderms. The estimated length of the individual is ~6.6m.

Key words: *Mourasuchus*. Crocodylia. Nettosuchidae. Miocene. Venezuela.

RESUMO: Notas sobre um esqueleto parcial de *Mourasuchus* (Crocodylia, Nettosuchidae) do Mioceno Superior da Venezuela.

O espécime MCC 110-72V depositado no Museo de Ciencias Naturales de Caracas, Venezuela, é aqui descrito. Este material, um esqueleto associado, mas incompleto, provavelmente um espécime de *Mourasuchus arendsi*, é proveniente da Formação Urumaco. Foi coletado no ano de 1972 em trabalho de campo conjunto entre instituições da Venezuela e da América do Norte. Os ossos estão mal preservados, todos os elementos tendo sofrido intemperismo químico durante a exposição em superfície e o processo diagenético. A litologia, no sítio, é descrita como um folhelho cinza com alto teor de gipsita. O espécime consiste de crânio e mandíbula, grande parte de coluna vertebral, fragmentos de costelas, partes das cinturas pélvica e escapular e alguns osteodermas. O comprimento estimado do indivíduo é de aproximadamente 6.6m.

Palavras-chave: *Mourasuchus*. Crocodylia. Nettosuchidae. Mioceno. Venezuela.

INTRODUCTION

An aberrant “duck-faced” crocodylian from the Pliocene of Brazil was named *Mourasuchus amazonensis* by PRICE (1964). Later, unaware of Price’s work, LANGSTON (1965) described *Nettosuchus atopus*, a similar animal from the middle Miocene Laventan stage (Honda Group) in Colombia (not the now questionable older “Friasian” South American Land Mammal Age as earlier reported by Langston, 1965): see FLYNN & SWISHER III (1995). Although the two taxa can be accommodated in one genus, they are significantly different at the species level, hence *Mourasuchus amazonensis* PRICE (1964) and *M. (=Nettosuchus) atopus* (LANGSTON, 1966). GASPARINI (1985) described *Carandaisuchus nativus*, a peculiar crocodylian with a pronounced tumescent bony occipital crest, from the late Miocene-Pliocene (Mesopotamiense) of Argentina, which is assignable to *Mourasuchus* (BOCQUENTIN &

SOUZA FILHO, 1990). A third species, *M. arendsi*, has been recognized by BOCQUENTIN VILLANUEVA (1984) from the upper Miocene (Huayquariense) Urumaco Formation of northern Venezuela (LINARES, 2004).

Mourasuchus is known largely from cranial material, but LANGSTON (1965) described the scapula and coracoid, the humerus, femur, ilium, and ischium of *M. atopus*, and BOCQUENTIN VILLANUEVA (1984) has described an incomplete articulated neck of *M. arendsi*. Here, I report additional postcranial material including, for the first time, osteoderms, of *Mourasuchus*, probably *M. arendsi*, from the Urumaco Formation.

Institutional abbreviations: CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; MCC, Museo de Ciencias Naturales de Caracas, Venezuela; UCMP, University of California Museum of Paleontology, Berkeley,

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California; UF, University of Florida, Florida Museum of Natural History, Gainesville, Florida; TMM, Texas Memorial Museum, The University of Texas at Austin, Texas.

RESULTS

DISCOVERY, OCCURRENCE AND CONDITION OF THE SPECIMEN

The specimen, MCC 110-72V, in the Museo de Ciencias Naturales de Caracas, Venezuela, is an associated but incomplete skeleton collected in 1972 by a joint field party from the Museum of Comparative Zoology at Harvard University, led by Dr. Bryan Patterson, in collaboration with the Escuela de Geología, Universidad Central de Venezuela and the Ministerio de Minas e Hidrocarburos de Venezuela (MEDINA, 1976; WOOD, 1976). The specimen consists of the skull and lower jaw, a substantial part of the vertebral column, fragments of ribs, parts of the pectoral and pelvic girdles, and some osteoderms of an individual with an estimated length of ~6.6m. Professor Patterson's unpublished field notes record that MCC 110-V72 and...“parts of a skull, jaws, vertebrae, etc “...of a “Giant crocodile” (111-72V) were found,...” weathering out of the same small projection from the west and south and from the east sides, respectively”. Thus, as Patterson noted, ...“some possibility of confusion exists”. Indeed, an incomplete right scapula lacking a field number, but accompanying MCC 110-72V, is larger than the scapulae belonging to that individual, and a humerus bearing number 110-72V is too small to belong with the *Mourasuchus* skeleton. The “Giant Crocodilian” MCC 111-72V is not further identified in the field notes. All the bones attributed here to MCC 110-72V are, however, concordant in size. Whether the remains were articulated when found is unknown, but the postcranial material was sent to me as separate unprepared elements. Differences in preservation and coloration of the bones suggest that they were somewhat scattered, but some vertebrae may have been articulated or were closely associated.

The locality is recorded as, “3¹/₂ km N 30°W of El Picacho, on the up side of the Chiguaje fault”, Falcon State (Patterson field notes, 1972). This places it about 6.5km N24°E of the town of Urumaco (Fig.1). The source bed may be a thin,

but extensive, stratum near the top of the upper member of the Urumaco Formation, informally referred to by field geologists as the “capa de tortugas” (=“capa de huesos”) because of its profuse fossil content (ROYO & GÓMEZ, 1960; PASCUAL & DÍAZ DE GAMERO, 1969; LINARES, 2004). There is some uncertainty about this, however, because Patterson's field notes specify many of the fossil occurrences in the area as coming from the “capa de huesos”, but MCC 110 72-V is not so noted. An additional complication is that a stratigraphic column of the Urumaco Formation giving positions of fossil occurrences (LINARES, 2004, p.9-10) shows Patterson's field numbers 103-115 lying some distance below the “capa de tortugas”, in the lower member of the Urumaco Formation. Moreover, on an accompanying map (Fig.2 of LINARES, 2004), Patterson's locality 103, which Patterson states is the same geographically as locality 110-72V, is shown south of Urumaco, in the opposite direction of locality 103 described in the notes. Resolution of this discrepancy is not possible here, so I follow the information provided in Patterson's notes. The approximate locality derived from a reading of the field notes includes a small outcrop of the “capa de tortugas” shown on the PASCUAL & DÍAZ DE GAMERO (1969) map (Fig.1). The lithology at the site is described as a gray, highly gypsiferous shale, which is characteristic of much of the Urumaco Formation. The rocks are believed to be of fluvial and lacustrine origin (LINARES, 2004). For further information about the origin, age, and paleoenvironment of Urumaco deposition, see DÍAZ-DE-GAMERO & LINARES (1989), LEV (1997), and LINARES (2004). The Urumaco Formation has yielded a diverse fauna of fossil fish, crocodilians, turtles, and mammals (LINARES, 2004; SANCHEZ-VILLAGRA *et al.*, 2004).

DESCRIPTION

The bones of MCC 110-72V are poorly preserved, all elements having suffered from chemical weathering during diagenesis and surface exposure. Superficial detail has been largely obliterated and often only a general idea of the external form of a bone can be discerned. Some bones are partly replaced by gypsum, as is usual among bones from the Urumaco region (BOCQUENTIN VILLANUEVA, 1984).

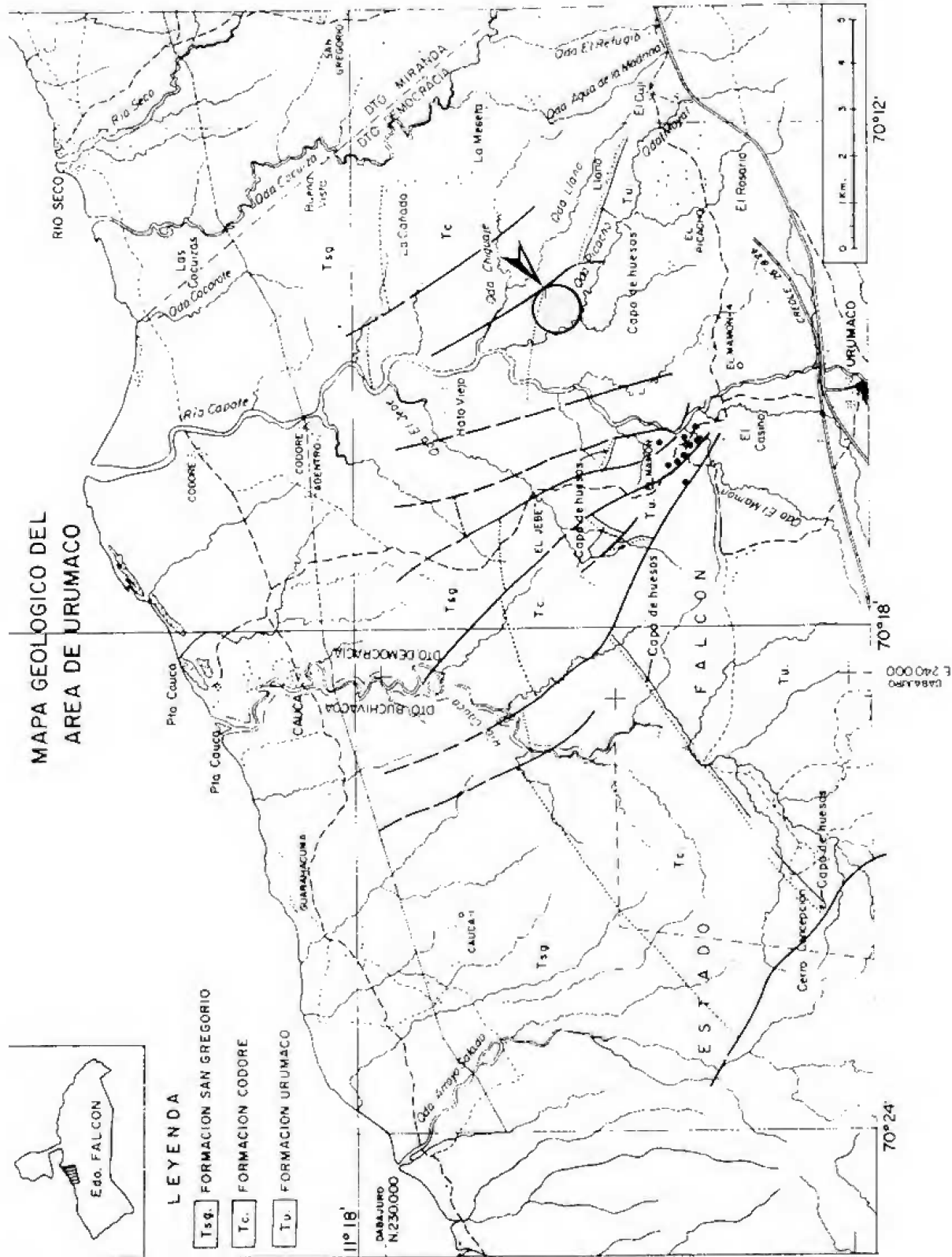


Fig. 1 - Simplified geologic map of the Urumaco area in northern Falcón State, Venezuela showing the "capa de tortugas" ("capa de huesos") and associated strata, prepared by geologists of the Texas Petroleum Company in 1958, and adapted from PASCUAL & DÍAZ DE GAMERO (1969). Large circle denotes approximate source area of *Mourasuchus arendsi* MCC 110-72V, deduced from field notes of Professor Bryan Patterson, 1972. Arrow points to a limited outcrop of the "capa de tortugas" which may include Patterson's locality 110-72V. The discontinuous outcrops of the capa de tortugas at the top of the Urumaco Formation (Tu) are indicated by the solid line labeled "Capa de huesos".

Axial Skeleton. The reconstructed skull and jaws of MCC 110-72V are currently on display at the Museo de Ciencias Naturales, Caracas, and have not been available to me. I am indebted to Dr. Ascanio Rincón (pers. comm., May 2005) for the following information about this specimen. The snout to quadrate length is 107cm (incorrectly reported as 1.25m by LANGSTON & GASPARINI, 1997), and the extreme width across the quadrates is 53cm; the width between the outer edges of the jugals is 50cm. The roof of each premaxilla is pierced by three rounded perforations.

Vertebrae are well represented, but reassembly of the vertebral column is conjectural. Only the atlas and axis, the two sacrals, and the biconvex first caudal are recognizable with certainty. Probably all of the cervical vertebrae are present, but the atlas is represented by its intercentrum only and the ninth cervical by a fragment of its neural arch. Four anterior and two posterior thoracic vertebrae, three lumbar, and thirteen caudals can be placed with some assurance. Two dissociated neural arches are likely from anterior thoracic vertebrae.

The atlantal intercentrum, viewed from below, displays the transverse constriction, or waist, observed in other eusuchians (Fig.2A). It is 49mm long and 71mm wide, caudally. The least width of the waist of the intercentrum is 53mm. On either side, caudally, a short caudolaterally projecting costal process bears a large asymmetrically

reniform facet 29mm wide and 18mm high for the head of the first rib. The processes are separated by a shallow transverse emargination in the caudal edge of the intercentrum 25mm wide, suggesting that the capitula of the atlantal ribs did not meet in the sagittal plane. The cranial cotyle is narrowly reniform in plan. It is 53mm wide and at least 36mm in dorsoventral diameter. A small tubercle of unknown function occurs on either side of the intercentrum a short distance behind the cranial edge of the occipital cotyle, and here the intercentrum expands briefly to a width of 57mm.

The axis and attached odontoid bone are badly corroded, and the dens are missing (Fig.2B-2C). The length, as preserved, of the combined odontoid and centrum (excluding the posterior condyle) is 70mm. The odontoid bone bears massive dia- and parapophyses (Fig. 2C, left). The diapophysis ends in a small facet, suggesting the existence of a bicipital axial rib. The cranially-facing trochlea that supported the dorsolateral hemiarches of the atlas are flat and the articular facets are nearly vertical (Fig.2C, left). The broken base of a prezygapophysis suggests that its articular facet for the atlantal postzygapophysis faced dorsolateral at approximately 45°. The ventral keel at the cranial end of the centrum is undivided, and is arched upward longitudinally in lateral aspect (Fig.2B-2C, left). The keel descends at its cranial end, forming a small hypapophysis, which is not forked *sensu* BROCHU (fig.51 of 1997).

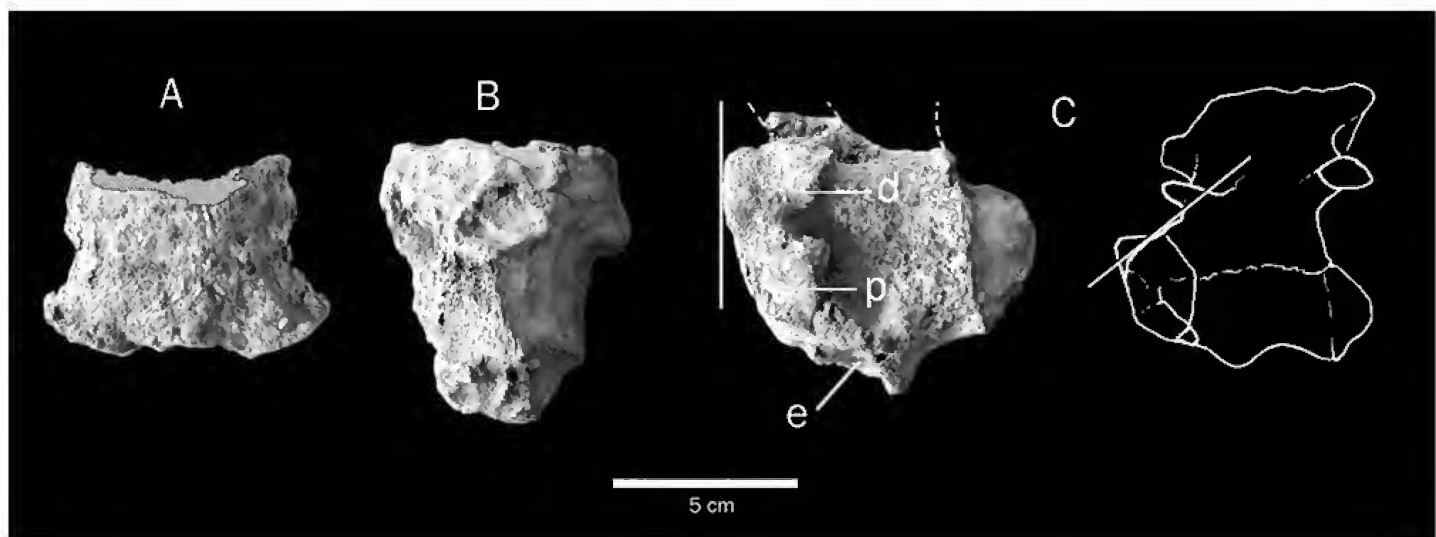


Fig.2- *Mourasuchus arendsi* (MCC 110 72-V), atlantal intercentrum, ventral view, anterior toward top (A), axis centrum with attached eroded odontoid bone, ventral view, anterior toward top (B), axis and attached odontoid seen from the left side (C, left), sketch of axis and attached odontoid bone of *Alligator mississippiensis* (C, right). d, diapophysis; e, eroded excavation at cranial end of hypapophysis; p, parapophysis. Straight lines indicate difference in inclination of the trochlear facets between *Mourasuchus* (left) and *Alligator* (right).

The cranial surface of the hypapophysis is excavated as though it lodged an ossicle, but this is probably an artifact of erosion. A lateral excavation about the size of a thumbprint occurs caudolaterally on the sides of the pedicles.

The centrum of the third cervical is 51mm long, excluding the condyle, 50mm high, excluding the hypapophysis, and 58mm wide behind the parapophyses (Fig.3A). The prezygapophyses project strongly upward, extending 10mm beyond the anterior plane of the centrum. The articular facets of the pre- and postzygapophyses slant toward the sagittal plane at an angle of 40°. The pedicle is almost as long as the centrum, excluding the condyle. A strong diapophysis bearing a hemispherical tubercular facet springs laterally from the centrum. The parapophysis, born low on the side of the centrum, is shorter and thicker than the diapophysis. The capitular facet is diagonally ovate, flat, and is larger than the tubercular facet.

The centrum of the fifth cervical is 56mm long, excluding the condyle, 59mm high, excluding the hypapophysis and 61mm wide at the cranial end (Fig.3C, left). A strong ventrolaterally-directed diapophyseal process springs from the lower part of the pedicel and the upper part of the centrum. Its relationship to the neurocentral suture is undetermined. The parapophysis, which arises from the lower part of the centrum projects laterally and is more massive than the diapophysis. The articular facets of the prezygapophyses face upward at an angle of 43° to the sagittal plane.

Intact cervical neural spines are preserved only in the presumed third and fifth vertebrae. The spine of the third cervical is a broad plate-like lamina 41mm long at the base, and expanding longitudinally to 45mm at its top (Fig.3B). Its dorsal edge is gently convex upward anteroposteriorly. The neural spine of the fifth cervical has a shorter base than that of the third cervical, and is a little more than twice as high, measured from the top of the neural canal (Fig.3C, left).

The cervical hypapophyses are relatively small and blunt, and lack a cranially-directed hook-like process distally. The largest preserved hypapophysis occurs on the sixth cervical (Fig.3C, right). All preserved hypapophyses are followed by an upwardly arched sagittal ridge on the bottom of the centrum.

The supposed third thoracic vertebra bore its dia- and parapophysis on the transverse process, which arises high upon the side of the pedicel. The parapophysis is bent slightly downward distally. The centrum of this vertebra is ~59mm long, excluding the condyle, 47mm high, excluding the hypapophysis, and ~49mm wide anteriorly (measurements are approximate owing to destruction of the cortical bone). Inclination of the prezygapophyses is 57° from the sagittal plane. Of the preserved anterior thoracic vertebrae only one bears a hypapophysis, which is small and scalene in lateral aspect, the shortest side facing cranial.

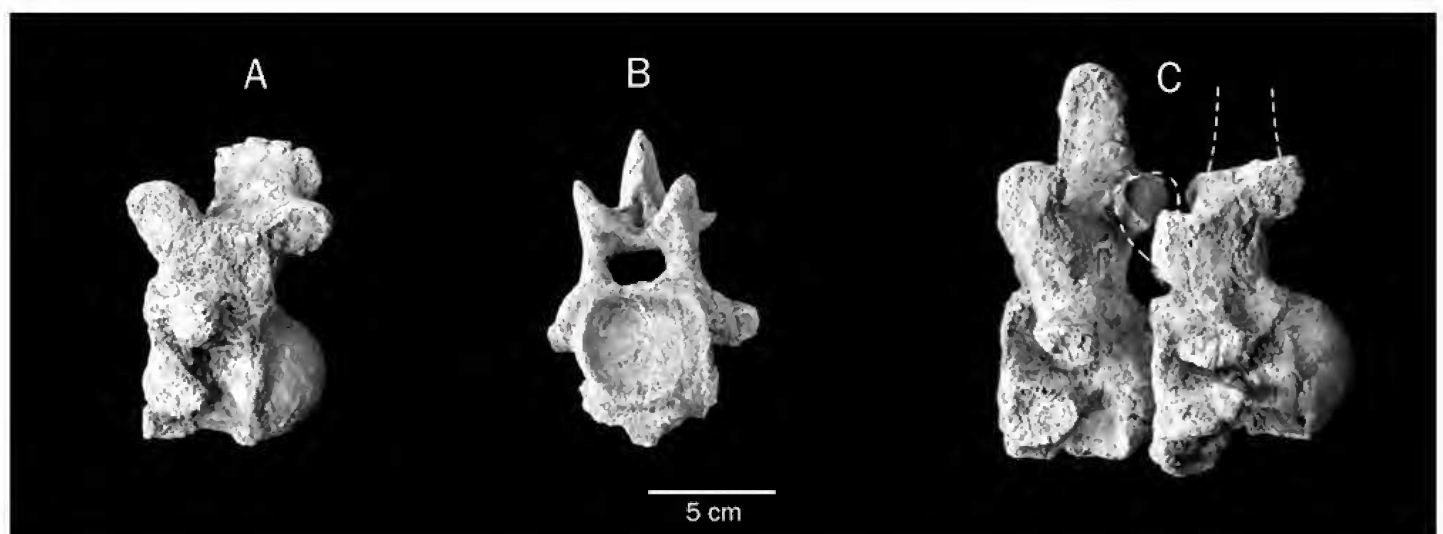


Fig.3- *Mourasuchus arendsi* (MCC 110 72-V), third cervical vertebra, lateral (A) and anterior (B) views; fifth and sixth cervical vertebrae, lateral view (C).

Two posterior thoracic vertebrae are larger than the anterior vertebrae. Their neural arches are wider and lower, and their centra are more cylindrical. The better preserved vertebra (Fig.4A) has a more gracile transverse process than the other, so was likely the more posterior of the two. It may have borne a single headed rib. The centrum is 67mm long, excluding the condyle, 60mm high anteriorly, and at least 65mm wide. The articular surfaces of the zygapophyses make an angle of 79° with the sagittal plane. There is a long shallow longitudinal excavation at about mid-height on

either side of the centrum and a deeper, smaller depression on the side of the pedicel bounded posterodorsally by a pronounced caudal centrodiapophyseal buttress. The base of the neural spine is 49mm long.

The lumbar series is represented by what are believed to be the first, third and fifth vertebrae. The centra of all three vertebrae are wider than high, the condyle of the supposed fifth lumbar being significantly wider than the others in relation to its height. The centrum of the putative first lumbar retains the spindle form associated with the thoracic series (Fig.4B).

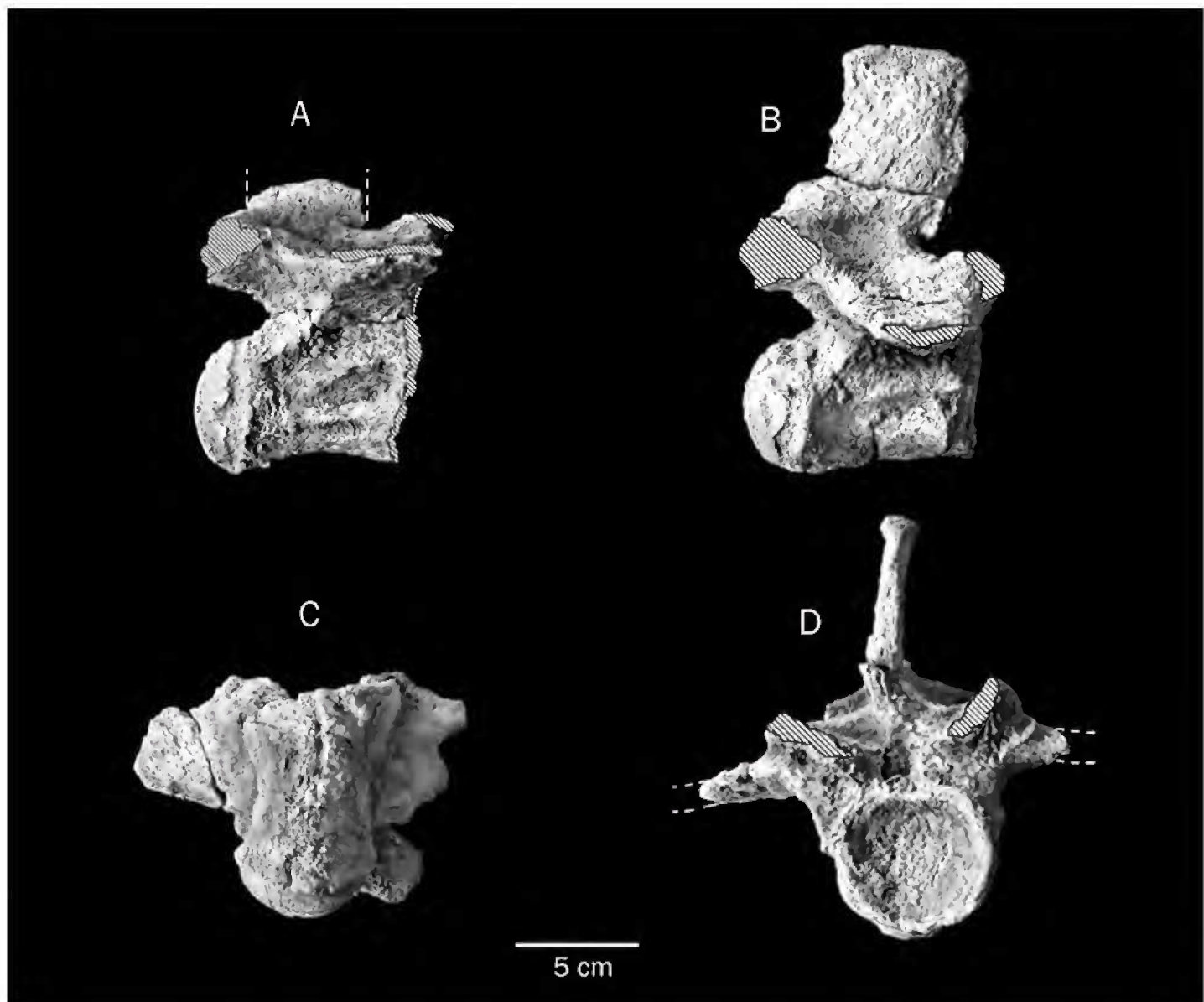


Fig.4- *Mourasuchus arendsi* (MCC 110 72-V), putative posterior thoracic vertebra, lateral view (A), putative first lumbar vertebra, right lateral view (B), ventral view, anterior toward top (C), anterior view (D). Note absence of “table top” expansion of the top of the neural spine.

It is 79mm long, excluding the condyle, 65mm wide and 55mm high cranially. It is about 57mm wide at mid-length. Corresponding measurements of the third lumbar are, respectively, 66mm, 70mm (e), and 59mm. Its width at mid-length is 62mm. The prezygapophyses make an angle of 48° with the sagittal plane in the first lumbar and of 50° in the fifth. The centrum of the first lumbar contains a shallow longitudinal fossa at about mid-height on either side (Fig. 4B-4C). Larger excavations are present on the third lumbar, but only shallow indentations occur on the fifth lumbar. The first and third lumbar retain intact neural spines (Fig. 4B, 4D). They are long based (anteroposterior diameters of 56mm), plate-like, and like other presacral spines lack “table-top transverse expansions at the tops. The spine of the first lumbar is 97mm high, measured from the top of the neural canal. The basal diameters of the lumbar transverse processes diminish caudad.

The cranial end of the first sacral is 83mm wide anteriorly and 61mm high (Fig. 5A, left). These dimensions for the second sacral are >56mm and 69mm, respectively (Fig. 5A, right). Articular faces of the postzygapophyses of the first sacral are transversely ovate, but those of the second sacral are broadly triangular and wider than high. The angle of inclination of the prezygapophyses of the first sacral is 58° to the sagittal plane, that of the postzygapophyses of the second sacral is about the same. The neural arches and centra of the sacral vertebrae are firmly fused to the sacral ribs. Viewed from above, the diapophyses of the first sacral obscure the underlying parapophyses, and the tuberculum of the first rib obscures the underlying capitulum. The lengths of the two sacral centra are, respectively, 107mm, and ~72mm. The sacrum is 100mm wide across the prezygapophyses of the first sacral vertebra and 59mm wide across the postzygapophyses of the second sacral. The bases of the first and second sacral neural spines are 75mm and 61mm long, respectively. Seen from the side, the distal (iliac) ends of the sacral ribs are as shown in figure 5A. The proximal end of the first sacral rib enters narrowly into the dorsolateral corner of the cotyl for the preceding lumbar vertebra. The second sacral rib resembles that of a large *A. mississippiensis* (TMM M-4864). The costal facets on the medial side of the accompanying ilium indicate that the ends of the sacral ribs did not meet distally. The transverse diameters across the attached sacral ribs are, respectively, 298mm and 229mm.

Thirteen caudal vertebrae, possibly constituting a continuous series, are present. In all, the neural

arches and caudal ribs appear to be solidly fused to their respective centra. Transverse processes are present on the last preserved caudal. Only the first caudal retains an intact neural spine, which is 59mm long at its base and 85mm high above the roof of the neural canal. Neural spines of all preserved caudals were long-based, that of the putative fifth caudal being 62mm long. The last preserved caudal is 80mm long, excluding the condyle, and the centrum is 41mm high at the cranial end. The transverse diameter of the centrum at mid-length is 23mm. Chevron facets first appear on the second and third caudals.

A noteworthy feature of these vertebrae is the absence of a bony sagittal web extending along the cranial and caudal edges of the neural spines. The sulci that sometimes accompany these webs at the base of the neural spines in the alligators and caimans are also absent in MCC 72-V (cf. Fig. 5B-5C).

The five cervical ribs preserved are unremarkable. Thoracic ribs are represented only by broken segments of the shafts. Sacral and caudal ribs are, described above.

Pectoral Arch. Both scapulae and coracoids are preserved, those of the right side being the more complete (Fig. 6, right). The scapula and coracoid are robust, a quality noted in the relatively small holotype of *M. atopus* (LANGSTON, 1965). The scapulae are missing the vertebral borders and parts of the edges of the scapular blades. When found, each scapula was connected *en matrice* with its respective coracoid, but the bones of the right side were displaced slightly at the scapulocoracoid interface. When separated in the laboratory these bones showed no evidence of bridging or fusion *sensu* (see BROCHU, 1995). What remains of the right scapular blade indicates that it did not flair appreciably above (see Fig. 51 of BROCHU, 1999). The constricted scapular “waist” is 57mm wide anteroposteriorly in the right scapula. There is no tuber caudalis scapulae (ROSSMANN, 2000). The broad scapular spine (deltoid crest of BROCHU, 1999 = crista cranialis scapulae of ROSSMANN, 2000) is thickened dorsally, but it thins rapidly toward the scapulocoracoid eminence. The edge of the spine is deflected caudally at the dorsal end, here forming a distinct tuberosity. The scapulocoracoid eminence is wide, extending 129mm from its most anterior point to the caudal edge of the glenoid fossa. The plan of the opposing articular surfaces of the scapula and coracoid is narrow longitudinally and its anteroposterior diameter is relatively long owing to the lengthening of the scapulocoracoid eminence.

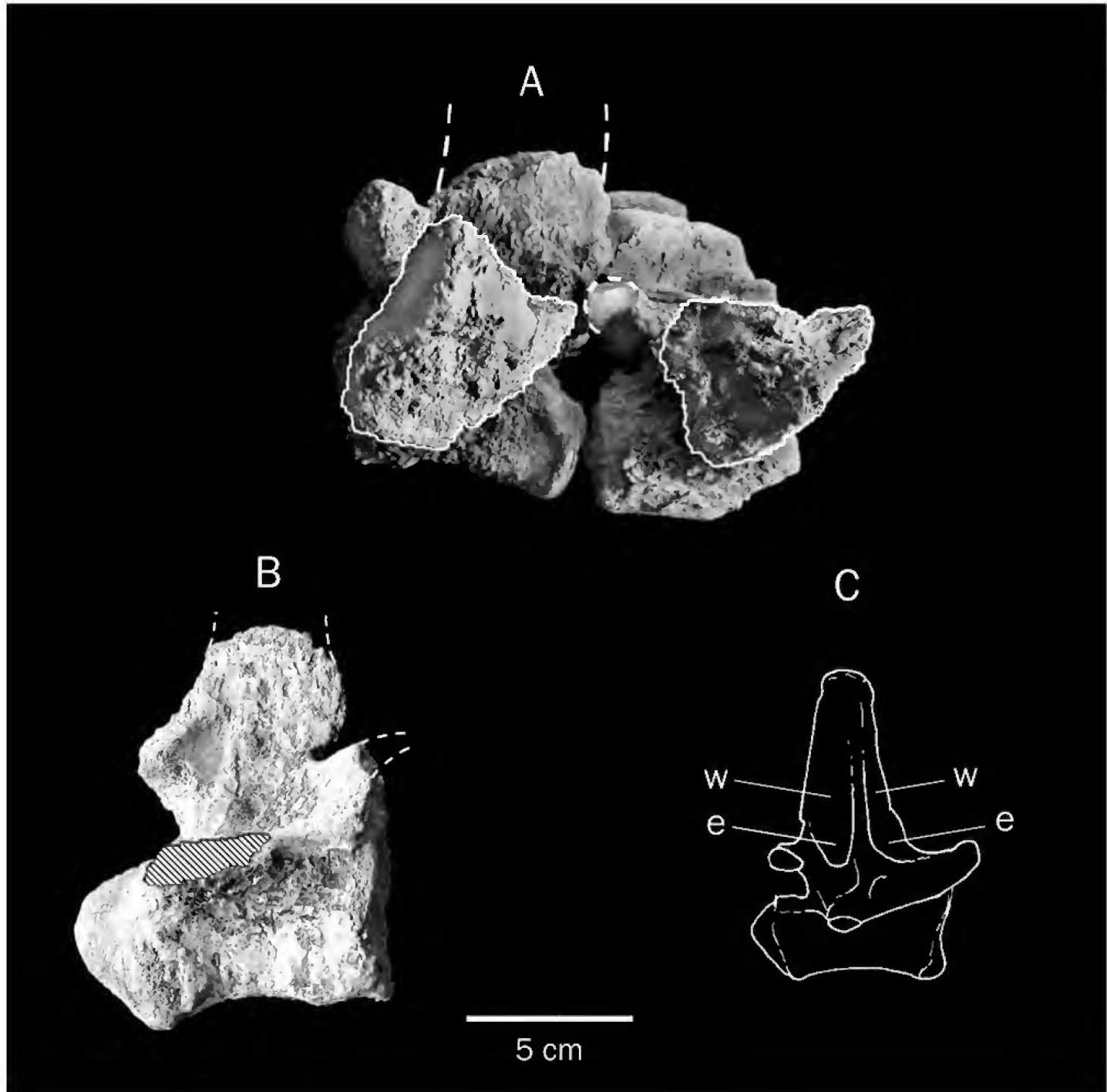


Fig.5- *Mourasuchus arendsi* (MCC 110 72-V), sacrum, left lateral view (A), the distal (iliac) articular surfaces of the sacral ribs are outlined. The narrow strip of bone seen above the broken base of the neural spine of the second sacral is the top of that vertebra's neural spine, which has been displaced and is largely hidden in this view. When restored to its natural position the spine is ~88mm high measured from the top of the neural canal, posteriorly. Right lateral view of the putative eighth caudal vertebra (B), note the absence of the spinous webs (w) and associated sulci (e) seen in neural spines of mid-caudal vertebrae of extant alligatorids, shown diagrammatically in *Alligator mississippiensis* (C).

The right coracoid (Fig.6, right) is 238mm long from the scapular edge to the sternal border. The scapular and sternal ends are, respectively, 139mm and 127mm long (anteroposteriorly). The least

anteroposterior diameter of the coracoid shaft is 56mm. Viewed from below, the transition from the scapulocoracoid eminence to the cranial edge of the coracoid blade is abrupt as compared to that

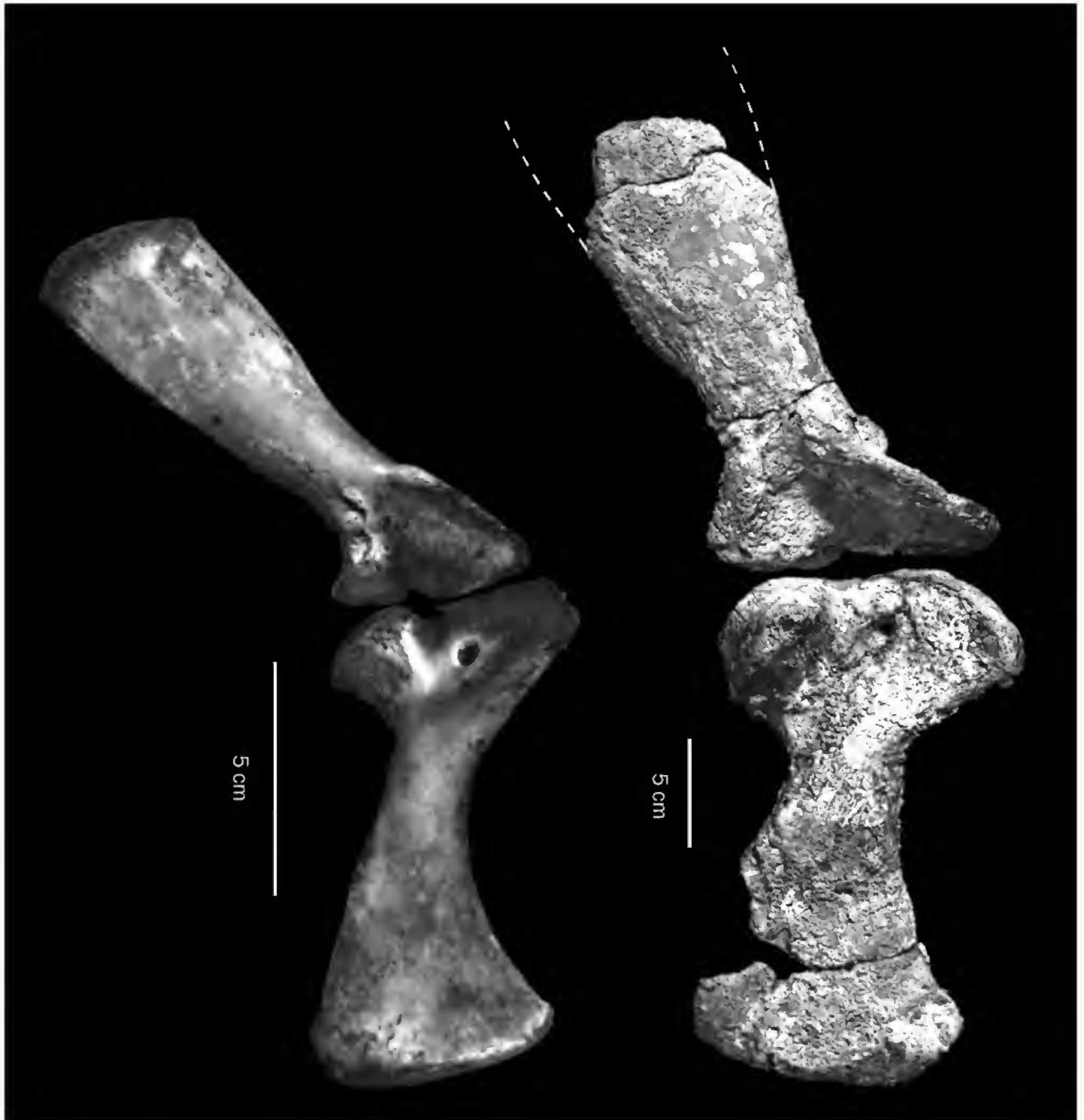


Fig.6- *Mourasuchus arendsi* (MCC 110 72-V), right scapula and coracoid. The bones are photographed in the same plane, e.g., they are not in their natural articulated relationship (right image). Corresponding bones of *Melanosuchus niger* (UF 72914) enlarged to same scale (left image) to emphasize the relatively short and robust nature of the fossil.

of *Caiman crocodilus*, for example (see Fig.51c of BROCHU, 1999). A round coracoid foramen with a diameter of 8mm occurs near the center of the proximal expansion of the coracoid. The coracoid

forms a little more than one-half of the glenoid fossa. The saddle-shaped articular surface of the fossa is broadly and deeply concave in the transverse direction and strongly convex

anteroposteriorly. It is 87mm high and 22mm deep. *Pelvic Arch.* The right ilium is badly eroded, the outer surface of the bone having been almost completely destroyed by chemical weathering. An overlay of the outline of the specimen upon the perfectly preserved ilium of the holotype of *M. atopus*, UCMP 38012 (Fig. 24 of LANGSTON, 1965), shows reasonable concordance between the bones (Fig. 7A). Like the ilium of *M. atopus*, there was a prominent anterior iliac process, represented by its broken base. A supraacetabular crest is essentially absent. The facets on the medial surface of the ilium for attachment of the sacral ribs are narrowly separated. The ilium is 113mm long at its narrowest diameter and 135mm high from the ischiadic peduncle to the top of the iliac blade.

An incomplete right ischium is 202mm long, but is otherwise uninformative.

Osteoderms. Fifteen osteoderms were found with MCC 110-72V. Although they convey an accurate

idea of their gross form, most examples have a concretionary coating of gypsum, which obscures surface details. Gypsum has partly infiltrated and sometimes replaced the bony substance. The largest osteoderm is a broad subround plate 98mm long and 101mm wide, with a broadly rounded, 38mm high paramedian elevation caudally (Fig. 8A, 8E). The elevation decreases gradually cranial. The deep face of this osteoderm is slightly arched transversely beneath the elevation, producing the "angulation" of HUXLEY (1860). One longitudinal edge is almost straight and is thus probably medial. Longitudinal edges are rounded dorsoventrally and are about 7mm thick. It is unclear whether either edge is serrated. The cranial edge is not noticeably beveled (faceted) for shingling by a preceding osteoderm. A slightly smaller and much thinner, weathered osteoderm has a basal plate which bears the base of a longitudinal crest lying somewhat to one side of the midline of the osteoderm.

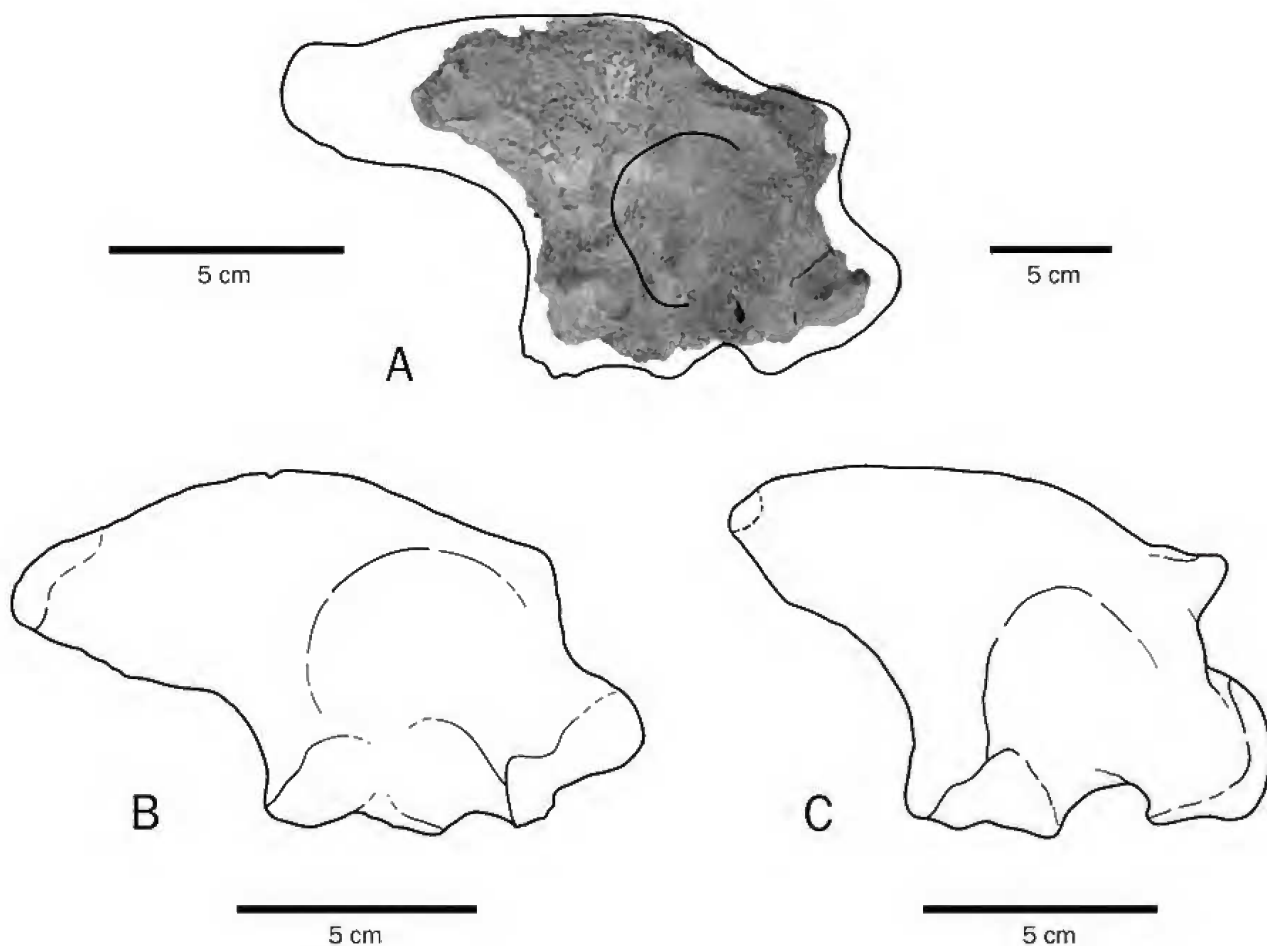


Fig. 7- *Mourasuchus arendsi* (MCC 110 72-V), right ilium, lateral view, right scale, compared to ilia of *M. atopus* holotype (UCMP 38012) solid outline adjusted to best fit, left scale (A), *Alligator mississippiensis* (TMM M-8931) (B), *Melanosuchus niger* (UF 72914) (C).

One other relatively large osteoderm has an irregular cardiform basal plate which bears a massive crest (somewhat distorted by crushing). The deep side of this osteoderm is downwardly convex, having no angulation. The edges are without sutures. A fourth osteoderm, about one-third as large as the first, bears a relatively more pronounced, thick and blunt parasagittal crest on the caudal half of the plate (Fig.8B, 8F). When seen from either end, this osteoderm displays an asymmetric or "twisted" gabled appearance, thus resembling a slightly skewed peaked roof. The angulation is 130° . Edges appear to be non-sutural and lack evidence of serial shingling. The external surface of this osteoderm is marked by small shallow pits and grooves radiating from the crest.

Other osteoderms have an expanded, more or less rounded, non-sutural basal plate, and a remarkably hypertrophied longitudinal crest (Fig.8D, 8H). The deep sides of these plates are flat or slightly convex

downward. Crests vary from broadly oval to laminar in planar cross section. The cranial edge of the crests is always longer than the caudal edge, giving the crest a swept-back appearance. One such osteoderm, which may be considerably altered by weathering (Fig.8C, 8G), has a relatively small basal plate bearing a wide and thin inclined crest which is 49mm long at the base, 56mm high and only 15mm thick at mid-height.

Two osteoderms are uniquely cornuted (Fig.9A-9D). The dorsal surfaces of the crests are strongly convex whereas the ventral side is flat, so the crest is bent slightly downward, distally. The crests are constricted circumferentially at their base, appearing somewhat tumid outward from the constriction and resembling a stubby horn rather than a carinated crest. The basal plate is roughly triangular in plan. In one such osteoderm the plate is expanded dorsally, forming a flange-like structure whose edges bear a few blunt serrations (Fig.9E).

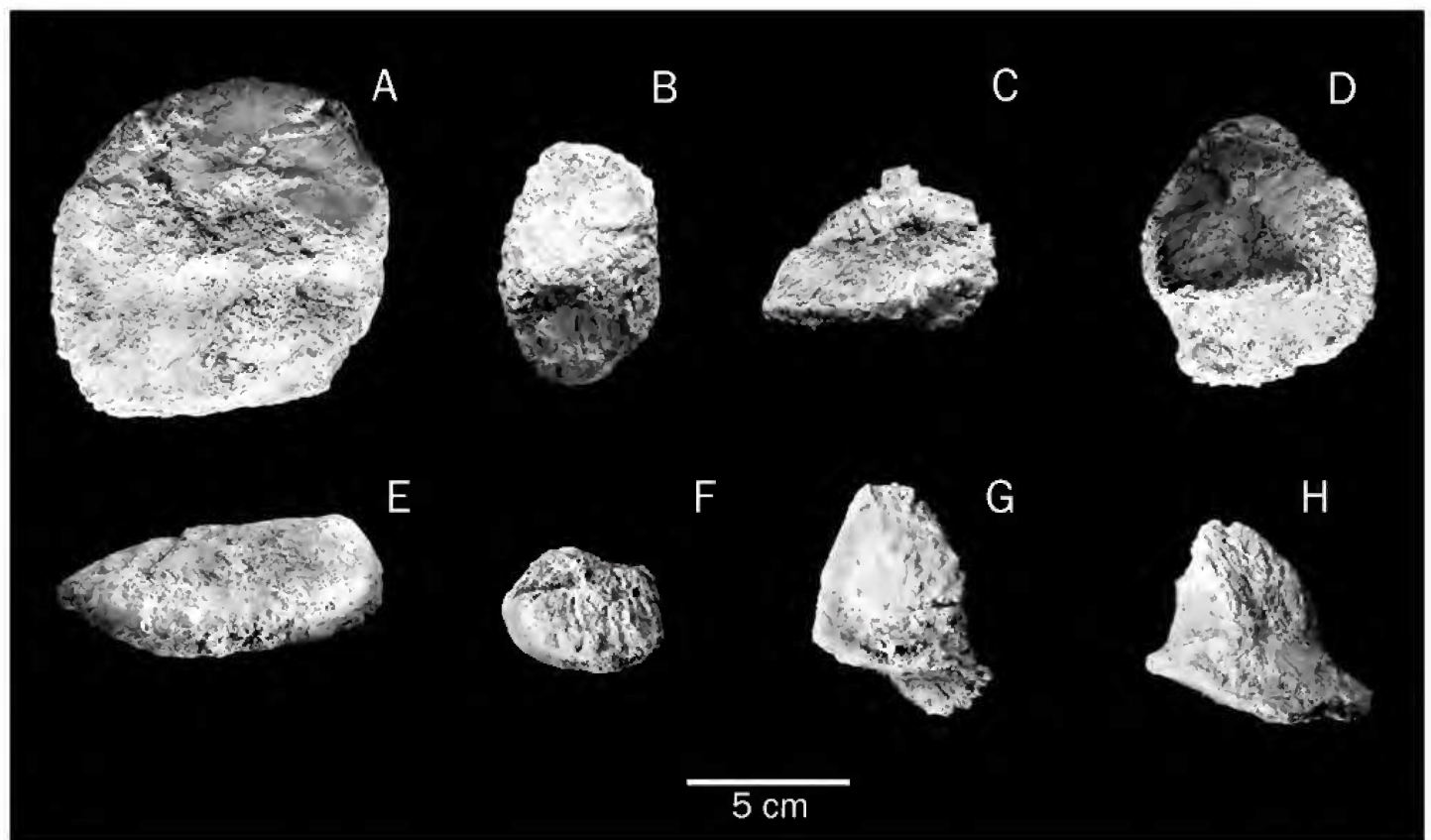


Fig.8- *Mourasuchus arendsi* (MCC 110 72-V), osteoderms, apical view (A-D), and lateral view (E-H). Possible first median right plate of the cervical shield or rosette (A, E) -the straight edge may be medial, the apex of the broad low crest is to the right-, asymmetric "gabled" osteoderm, possibly from the occipital group or a lateral member of the cervical rosette, anterior is to the right (B, F), osteoderm of unknown position with small basal plate and large thin (tabular) crest (C,G), possible flank osteoderm with large caudally curved crest, anterior edge is to the right (D, H).

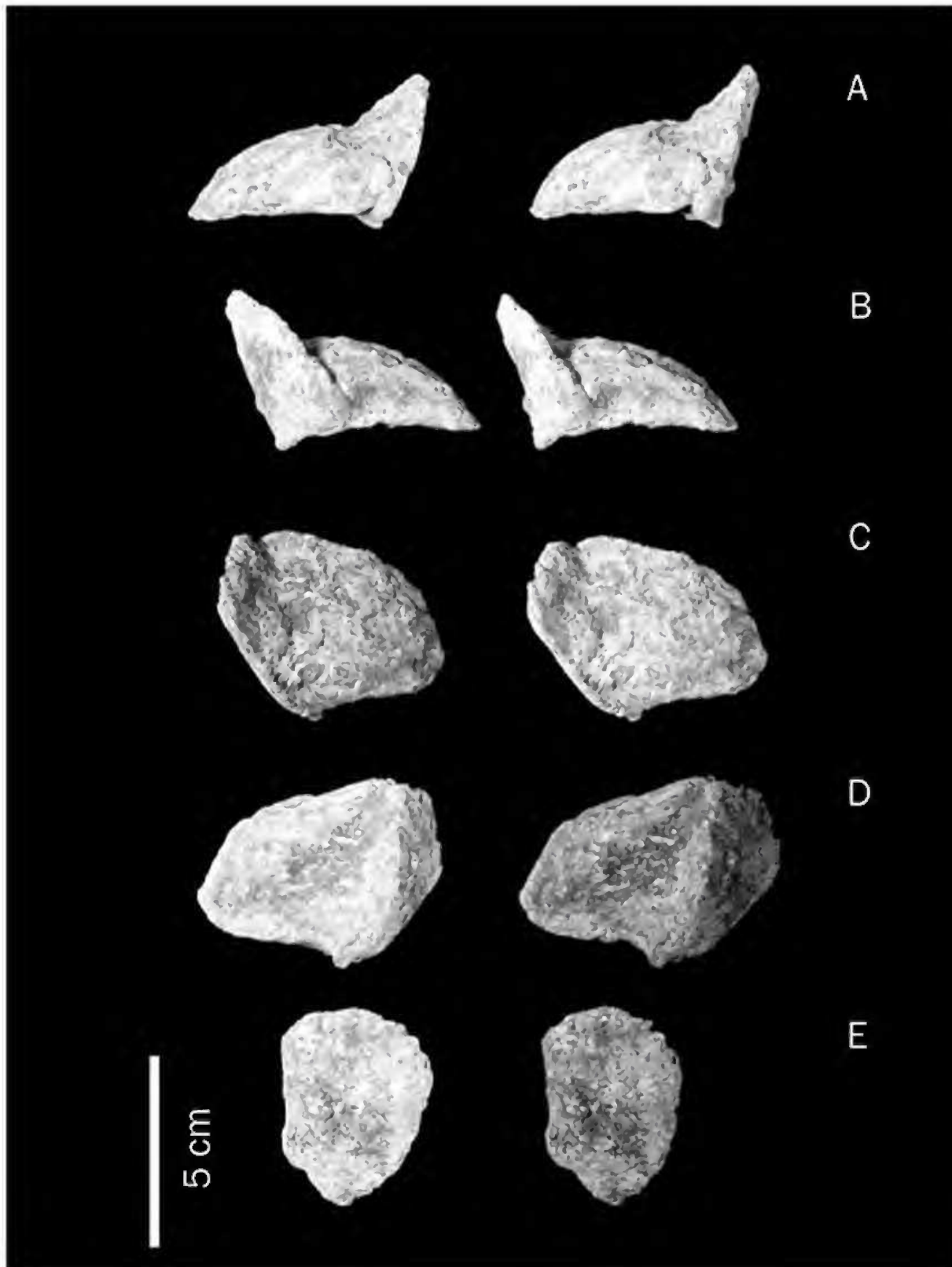


Fig.9- *Mourasuchus arendsi* (MCC 110 72-V), stereo images of an unique horn-like osteoderm, possibly from a right lateral longitudinal series, anterior view (A), posterior view (B), apical view (C), anterior is at top, ventral view (D), anterior is at top, deep surface(E), anterior is at top. Note blunt marginal processes along anterolateral edge.

The serrations, instead of forming a sutura serrata or a sutura dentata are apparently outgrowths that were imbedded in the dermis. The corresponding edges of the other horn-like osteoderm are abraded and show little evidence of serrations. The dorsal surface of the horn-like process appears to have a few short corrugations extending parallel with the long axis of the crest and exiting along the crest's lateral edge.

DISCUSSION

Systematic position. MCC 110-72V accords with 16 of 29 character states scored by BROCHU (1999) as present in *Mourasuchus* (five states having to do with ribs and osteoderms are not observable in *Mourasuchus* specimens). Five states queried by Brochu owing to insufficient or absent data are clarified by 110-72V, and two scores are revised (Tab.1). BROCHU (1999) scores number 34, the anterior iliac process (=Tuber cranialis iliacum of ROSSMANN, 2000), as virtually absent (1) in his matrix. I would score it as prominent, based upon the well preserved ilium of *M. atopus* UCMP 38012. The remnant of the process preserved in MCC 110-72V is relatively even larger than the corresponding feature in UCMP 38012. None of the findings reported here alter the placement of *Mourasuchus* within the Caimaninae proposed in BROCHU's (2004) cladistic analysis of the

alligators, but further study of *Purussaurus* and especially the enigmatic *Orthogenysuchus* may remove these as sister taxa of *Mourasuchus*.

BROCHU (1999) scores the anterior iliac process (=Tuber cranialis iliacum of ROSSMANN, 2000) as virtually absent (1). I would, however score it as present, based upon the ilium of *M. atopus* UCMP 38012. The remnant of the process preserved in MCC 110-72V is relatively even larger than the process in UCMP 38012, and to my eye easily qualifies as prominent, though less hypertrophied than in *Gavialis* (Brochu, pers.com., 2007). Interestingly, notwithstanding extensive osteological evidence supporting the alligatoroid affinity of *Mourasuchus*, the ilium of *M. atopus* (UCMP 38012) and of MCC 110-72V (Fig.7A) resemble the bone in such non-alligatoroid taxa as *Gavialis gangeticus* and some species of *Crocodylus* (Fig.29A, 29B of BROCHU, 1999). A robust anterior process, for example, which generally lies in apposition to, or extends a short distance beyond, the anterior dorsolateral corner of the first sacral rib described by BROCHU (1999) as "almost lacking" in alligatoroids, excepting *Paleosuchus trigonatus* (Fig.29D of BROCHU, 1999) and *Melanosuchus niger* (Fig.7C) is strongly developed in both *Mourasuchus* species (Fig.7A). The iliac blade in the holotype of *M. atopus* and probably also in MCC 110-72V is narrower dorsoventrally than in *A. mississippiensis*, *Melanosuchus* (Fig.7A-7C) or *Diplocynodon hantoniensis* (Fig.29E of BROCHU, 1999),

TABLE 1. Modifications to BROCHU's 1999 matrix of *Mourasuchus* required by the present study.

NUMBER	DESCRIPTION	BROCHU	110 72-v
6	Axial hypapophysis toward center (0) or toward anterior end (1) of centrum	?	1
13	Anterior sacral [rib] capitulum projects far anteriorly of tuberculum, broadly visible from above (0), or capitulum and tuberculum nearly coextensive anteriorly, capitulum largely obscured from above (1)	?	1
22	Scapular blade flares dorsally at maturity (0) or edges of blade sub-parallel at maturity (1)	?	1
24	Scapulocoracoid chondrosis closes very late in ontogeny (0) or relatively early in ontogeny	?	0
28	Dorsal margin of iliac blade rounded with smooth border (0) or rounded with modest dorsal indentation (1) or rounded with strong dorsal indentation "wasp-waisted" (2) or narrow with strong dorsal indentation (3) or rounded with smooth border, posterior tip of blade very narrow (4)	3	2
34	Anterior iliac process prominent (0) or virtually absent (1)	1	0
36	Dorsal midline osteoderms rectangular (0) or square (1)	1	?

The numbers in the left hand column correspond to the serial numbering in Brochu's Appendix 2: "List and Matrix of Characters Used in Phylogenetic Analysis". Language under DESCRIPTION has been slightly altered for the sake of brevity. The two right hand columns are the original and revised scoring, respectively, for *Mourasuchus* resulting from the study of MCC 110 - 72V and two corrections (numbers 28 and 36) based on UCMP 38012 (*M. atopus*).

and is more comparable with the ilium of *Crocodylus acutus*. It is, however broader than the blade in *P. trigonatus* (Fig. 29D of BROCHU, 1999), which has the narrowest blade among alligatoroids. The posterior end of the blade is deflected downward in the holotype of *M. atopus*, which resembles the condition in *C. acutus* and *P. trigonatus*. This feature is not preserved in MC 110-72V.

Comparisons. The Nettosuchidae comprises *Mourasuchus atopus* (Langston, 1965), *M. arendsi* Bocquentin Villanueva, 1984, *M. nativus* (Gasparini, 1985), and *M. amazonensis* Price, 1964. From descriptions in the literature it seems clear that the first three taxa are more similar to each other than they are to *M. amazonensis*. BOCQUENTIN VILLANUEVA (1984) and BOCQUENTIN & SOUZA FILHO (1990) have satisfactorily differentiated *M. arendsi* from the other nettosuchids.

The skull of the holotype of *M. arendsi* (CIAAP 1297) and MCC 110-72-V are approximately the same size, but the rostrum and the laterally expanded jugals appear relatively wider in photographs of MCC 110-72V than portrayed in drawings of CIAAP 1297 (Fig. 1 of BOCQUENTIN VILLANUEVA, 1984), which seems closer to the skull of *M. atopus* (UCMP 38012) – see figure 28 in LANGSTON (1965). Such differences may, however, result from artificial dorsoventral flattening and consequent lateral displacement of cranial bones in MCC 110-72V. The sides of the rostrum are roughly parallel, as in *M. arendsi* and *M. atopus*.

As reconstructed, each premaxilla of MCC 110-72V is pierced dorsally by three round perforations (for the tips of dentary teeth), one fewer than in *M. arendsi* CIAAP 1297, and one more than in *M. atopus* UCMP 38012. Differences in number and arrangement of such foramina may represent individual variation as seen, for example, in *Caiman crocodilus* (cf. fig. 25 in KÄLIN, 1933), or they may be ontogenetically related.

The intercentrum of the atlas is relatively shorter than that of *Alligator mississippiensis*, *Melanosuchus* and *Caiman crocodilus*, consistent with other evidence of a relatively short neck in *Mourasuchus*.

The cervical vertebrae of MCC 110-72V are larger than those of an articulated series of cervicals found adjacent to the holotype skull of *M. arendsi* (CIAAP 1297). The least transverse diameter of the atlantal intercentrum in that specimen is 35mm compared to 53mm in MCC 110-72V. BOCQUENTIN VILLANUEVA (1984) records the width of the sixth cervical centrum in CIAAP 1297 as 47mm and the length of the centrum as 57mm, including the condyle.

Based on the drawing and scale given by BOCQUENTIN VILLANUEVA (1984, Fig. 2B), exclusion of the condyle would reduce this length to about 38mm. Corresponding measurements for the sixth cervical centrum of MCC 110-72V are: width, 58mm behind the root of the diapophysis (62mm at the cranial end of the centrum) and a length of 51mm, excluding the condyle, or about 1.3 times the size of CIAAP 1297.

The discrepancy in size of the cervical vertebrae between two animals with similar head lengths is difficult to explain and recalls Patterson's field notation that two specimens were found weathering from opposite sides of the same hill at his Locality 110-72V. It raises the possibility that either MCC 110-72V or CIAAP 1297 is composite. This notwithstanding, such limited morphological comparisons as can be made between MCC 110-72V and CIAAP 1297, e.g., the proportionally short cervical centra, the low neural spines and the absence of cranially hooked distal ends on reduced hypapophyses supports their assignment to the same taxon. (The geographic proximity and stratigraphic context – "capa de tortugas" – upper Miocene, upper Urumaco Formation – in northern Falcón State, Venezuela, accords with this conclusion).

The scapula and coracoid are more robust than in extant Alligatoridae and Crocodylidae (Fig. 6). For example, in samples of *A. mississippiensis* (n=9) and *Crocodylus* spp. (n=7) the average ratio of least anteroposterior diameter of the coracoid shaft to the length of the coracoid is .17 and .15, respectively, whereas the corresponding ratio in MCC 110-72V is .24. Corresponding ratios in *Gavialis* (n=3), *Melanosuchus* (n=1), and *Tomistoma* (n=1) are, respectively, .13, .18, and .15.

Ontogenetic stage. The large size of MCC 110 72-V raises a question about the ontogenetic stage of the individual. Attempts to "age" the specimen using growth marks in an osteoderm (BUFFRÉNIL, 1980; ERICKSON & BROCHU, 1999) proved futile owing to diagenetic disturbance of the bone tissue. A total of 15 sequential annuli were counted in one thin section and additional fragmentary growth marks are scattered about randomly, but correlations between them are impossible.

Except, possibly, on the axis vertebra, neurocentral sutures are not discernable. Although some of the neural arches were found separated from their centra, the separation occurs at fractures through the pedicels, suggesting that the neurocentral sutures were closed or fused (BROCHU, 1996).

The articulation between the damaged odontoid bone and the centrum of the axis vertebra is either closed or fused to the axial centrum, forming a unitary epistropheus. These facts suggest that MCC 110 72-V was ontogenetically mature at time of death.

Size and proportions. *Mourasuchus* was a large crocodylian. Known skulls of *M. arendsi* are approximately 1m long, depending upon the definition of "total skull length" used by various authors. Among several proposed methods for estimating total body length of crocodylians based upon skull length (e.g., MEYER, 1984; COTT, 1961; WOODWARD *et al.*, 1995), a graphical solution by WERMUTH (1964, Fig.5) is useful in the absence of conclusive information about the shape of the post-cranial body of *Mourasuchus*. Wermuth arranged all extant crocodylian species into six groups based upon the length of the head relative to total body length. Although the shape of the rostrum of *M. arendsi* is unique, the skull as a whole is proportionally comparable in length and trans-quadrangle width to the skull of *Gavialis gangeticus* with a similar trans-quadrangle width. It should therefore fall into Wermuth's Group VI, comprising *G. gangeticus*, *Tomistoma schlegelii*, and *Crocodylus johnsoni*. From Wermuth's graph it is seen that MCC 110-72V should have been in the neighborhood of 6.6m long at the time of death. This estimate is slightly below values obtained from commonly used ratios of head length: total body length as, e.g., 1:7.48 for *C. porosus* (WERMUTH, 1964) and 1:7.5 for *C. niloticus* (BELLAIRS, 1970). It is worth noting here that BELLAIRS (1970) obtained a head: length ratio of about 1:5 for *G. gangeticus*, owing to its relatively long rostrum.

Estimation of body mass for MCC 110-72V is even more conjectural as it depends upon the determination of body length. Recent work (FARLOW *et al.*, 2005) shows that the relationship between body length and mass based on *Alligator mississippiensis* predicts sizes of extant crocodylian species reasonably well, and may be used to estimate the mass of related species in the fossil record. An extrapolation from a FARLOW *et al.* (2005) graph, figure 7A, yields a mass value of 1,400kg for the 6.6m long MCC-110V. Farlow's regression (pers.comm., June 13, 2005), based on data from 58 captive alligators yielded a mass of 1,634kg ($R=0.995$, $P<0.001$). WEBB & MANOLIS (1989) quote an "average" body weight of 6m long *Crocodylus porosus* from tidal rivers as 900kg. Crocodylians in captivity may bulk larger than wild animals of similar lengths, so mass values between 1,400kg

and 1,634kg for MCC 110-72V seem reasonable.

Head and neck motility in *Mourasuchus*. The character of the cervical vertebrae described above bespeak of a relatively weak and less motile neck than that possessed by extant crocodylians. As noted by BOCQUENTIN VILLANUEVA (1984) the cervical vertebrae are, indeed, relatively shorter than those of extant crocodylians. Measurements of MCC 110-72V show that the average ratio of least width of centrum to length of centrum, excluding the condyle, for cervicals 3-6, is 0.95. The largest value for any cervical in this specimen is 0.98. Corresponding ratios for available extant taxa are: *Alligator mississippiensis*, 1.29 (n=5), *Melanosuchus niger*, 1.49 (n=1), *Tomistoma schlegelii*, 1.31 (n=2), *Crocodylus acutus*, 1.28(n=5), and *C. cataphractus*, 1.24 (n=1). The average ratio among these taxa is 1.36, no value for an individual being less than 1.0. The more nearly vertical trochlear surfaces on the odontoid bone indicate a shorter vertical excursion of the head than is achieved in extant crocodylians. The small non-hooked hypapophyses suggest less development of the *M. longus colli*, which is involved with flexing and lateral movement of the neck (RICHARDSON *et al.*, 2002). The low cervical spines suggest that the epaxial antagonists were also less powerful than in extant taxa. Consistent with the foregoing, BOCQUENTIN VILLANUEVA (1984) states that the occipital condyle is small in *M. arendsi* (CIAAP 1297).

Thus, *Mourasuchus* was likely less capable of the violent head movements during capture and dismemberment of prey than are observed in large contemporary crocodylians.

Prey and Feeding. The present study offers added support to previous speculations (e.g., LANGSTON, 1965) on possible feeding strategies of *Mourasuchus*. The animal was likely a "lie in wait" predator inhabiting quiet waters and subsisting on "sluggish" fish (e.g., *Lepidosiren*, some catfish), whose remains have been encountered in the vicinity of *Mourasuchus* sites in Colombia, especially in the Fish Bed in the lower part of the Villavieja Formation of the Honda Group (LANGSTON, 1965; LUNDBERG, 1997), and freshwater crabs, in the Urumaca area (Patterson, 1972, field notes; Langston, 2005, personal observation).

Osteoderms. The exact positions of the fossil osteoderms in the living *Mourasuchus* are, of course, unknown. The two largest osteoderms found with MCC 110-72V may, however, belong to the cervical shield or rosette (RICHARDSON *et al.*, 2002),

which contains the largest osteoderms in extant crocodylians. The larger of the two plates is substantially more massive than any others recovered with MCC 110-72V. Its proportions, its apparently non-embroccating caudal edge, and its single straight longitudinal edge suggest that it may be the first median right osteoderm of the rosette. A slightly smaller, flatter plate with a more laterally placed crest may be the left medial osteoderm of the second transverse series of the rosette. A much smaller, angulated and “twisted” plate (Fig.8B, 8F) may be from the edge of the rosette as it is thick, has only a low, broadly rounded crest, lacks sutural edges and shows no evidence of shingling. But, these features might also place it among the occipital osteoderms which lie in the soft skin between the transverse occipital crest of the skull and the cervical rosette.

The osteoderms with more elevated crests arising from more or less discoid bases without angulations, sutural or imbricated edges, may represent accessory plates, but their elevated crests render them considerably more spinose than osteoderms in extant crocodylians. The crests are more in keeping with the articulated transverse series of osteoderms in the dorsal shield of extant crocodylians. If these are, in fact, from the dorsal shield, their lack of sutured edges and shingling indicate that they did not form a cohesive armor like that of extant caimans, s.l. (*vide* HUXLEY, 1860).

The remarkable horn-like osteoderms of *Mourasuchus arendsi* described above may represent a lateral fringe extending longitudinally along the flanks of the animal – an aëtosaurian model springs to mind. This analogy cannot be drawn too narrowly, however, as the *Mourasuchus* osteoderms were non-embroccating and without sutures.

Of known crocodylians, only the Paleocene eusuchian *Acanthosuchus langstoni* O’Neill, Lucas & Kues, 1981, and the tiny, poorly understood Upper Cretaceous *Pinacosuchus mantiensis* Gilmore, 1942 possessed osteoderms with spike- or horn-like osteoderms. The only known specimen of *A. langstoni*, includes among others, more than 120 osteoderms with spike-like crests, evocative of aëtosaurian architecture. The horn-like osteoderms of *Mourasuchus* resemble somewhat those of *Acanthosuchus*, but they are more rotund than in the smaller taxon. They agree in the absence of embroccating facets, however. *Acanthosuchus* osteoderms do not have the annular constriction seen at the base of the crests in *Mourasuchus*. The basal plates of the spiked

osteoderms in *Acanthosuchus* are square to round and display a radiating system of buttresses around the base of the spikes not seen in *Mourasuchus*. The *Acanthosuchus* plates bear limited sutures on one parasagittal edge, suggesting coupled pairs, arranged into transverse rows. O’NEILL *et al.* (1981) supposed, however, that the spiked osteoderms formed a single, “...row of paired scutes along each side of the dorsal surface of the body and tail”, in *Acanthosuchus*.

The spike-like crests on *Pinacosuchus* osteoderms are often placed asymmetrically and sometimes extend beyond the edges of the basal plates, unlike the crests of *Mourasuchus*, and spikes are described as having sculptured surfaces (GILMORE, 1942). Associated vertebral centra are biconcave, so the animal is not likely a eusuchian.

In his detailed account of crocodylian armor, especially that of *Melanosuchus (=Jacare) niger*, HUXLEY (1860) observes that the osteodermal armor of the Caimaninae (*Caiman*, *Melanosuchus* and *Paleosuchus*) is more extensive than that of other extant crocodylians. All laterally contiguous osteoderms of both the dorsal and ventral armor (the latter extensively present in extant crocodylians only in Caimaninae) are joined laterally by suture, the tail being completely encircled by articulated osteoderms. Excepting some osteoderms in the skin of the neck, the dorsal and ventral osteoderms are slightly imbricated in Caimaninae, posterior edges moveably overlapping narrow smooth transverse anterior facets on each succeeding osteoderm. Even the limbs [of *M. niger*] are, “...covered with articulating scutes...” (HUXLEY, 1860).

Although *Mourasuchus* is related to alligators and caimans, its armor seems, from the limited information available, to deviate substantially from the norm for those taxa. There is no evidence that *Mourasuchus* possessed ventral or appendicular osteoderms. Evidence that the osteoderms were joined by parasagittal suture, or that they overlapped is also lacking. Reduced armor as seen in *Crocodylus porosus* (Fig.7 in WERMUTH, 1953) has long been correlated with that taxon’s aquatic habits where the weight of armor might be disadvantageous, and increased trunk flexibility would be an advantage in swimming. By contrast, the supporting function of massive articulated osteoderms and the expanded tops of the neural spines to which the sagittal osteoderms are attached by ligaments (SALISBURY & FREY, 2001), as seen in some caimans and *A. sinensis* (*vide* HUXLEY, 1860; ROVERETO, 1912; MÜLLER, 1924), but absent in *Mourasuchus*, would seem

unnecessary in a crocodylian that only occasionally travels on land. Oddly, gain in freedom of movement in the trunk by reducing the dorsal armor seems counterintuitive to the idea of a longitudinal series of horn-like lateral osteoderms as proposed above. In life, however, lateral tensing of the trunk would have been governed by the space intervening between serially aligned osteoderms. The small size of the basal plates of the horn-like osteoderms of *Mourasuchus* suggests there may have been considerable separation between them in the skin, and lateral bending of the trunk would have been unrestricted.

Taphonomy. Early work by vertebrate paleontologists and later by GONZALEZ DE JUANA *et al.* (1980) implied that vertebrate fossils of the upper Urumaco Formation were largely concentrated in the “capa de tortugas”, but it is now known that fossils are more widely distributed both stratigraphically and geographically in a variety of lithologies (LINARES, 2004). It is still unclear, however, where in the section most of the Urumaco crocodylians have been found. More taphonomic information including the relationships between *Mourasuchus* and other organic remains, including trace fossils, is necessary for a better understanding of the behavior of *Mourasuchus*. For example, what were the makers (lungfish, catfish, crabs, etc.?) of the frequent vertical burrows reported by DÍAZ DE GAMERO & LINARES (1989) in the upper member of the Urumaco Formation. The environmental conditions that produced the “capa de tortugas” and the diversity of crocodylians within the region, and an analysis of individual burials in the upper Urumaco are other questions that should be addressed.

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